

REVISION OF *LOBELIA* SECT. *GALEATELLA*
(CAMPANULACEAE: LOBELIOIDEAE)

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ABSTRACT

Lobelia sect. *Galeatella* is a group of pachycaul treelets distinguished by a solitary pliestesial hapaxanthic shoot from a suckering rootstock; a dense apical rosette of sessile coriaceous leaves leaving a helical pattern of raised corky cicatrices on the unbranched stem; a branched or unbranched terminal short-pedunculate bracteate raceme of large ornithophilous flowers on ebracteolate pedicels; calyx lobes caducous from the young fruit; non-blue corolla with linear monomorphic lobes, the dorsal pair spreading or recurved horizontally, about as long as the stout tube to 3 times longer, the ventral connate for $\frac{2}{3}$ their length or more, forming a deflexed inrolled trifid lip shorter than the dorsal pair; staminal column exerted, all five anthers with apical tufts of white trichomes; apically loculicidal capsule enshrouded at maturity by an irregular network of sclerenchymatous bundles; and winged oblong compressed seeds with a faintly striate testa. The section is endemic to the Hawaiian Islands, with two species each on Kaua'i (*L. villosa* and ***L. wahiawa***, sp. nov.) and O'ahu (*L. gaudichaudii* and ***L. koolauensis***, comb. et stat. nov.), and a single species (*L. gloria-montis*) on Maui and Moloka'i, divided into two subspecies: subsp. *gloria-montis* (West Maui and Moloka'i) and subsp. ***longibracteata***, stat. nov. (West Maui and East Maui). The two species on Kaua'i hybridize, producing ***L. xkauaiensis***, stat. nov.

RESUMEN

Lobelia sect. *Galeatella* es un grupo de arbolillos paquicaules que se distinguen por su vástago solitario multiperenne monocárpico que surge de un rizoma adventicio; una roseta apical densa de hojas coriáceas que dejan un patrón helicoidal de cicatrices suberosas levantadas en el tallo sin ramas; un racimo bracteado terminal ramoso o no cortamente pedunculadote de flores grandes ornitófilas sobre pedicelos ebracteolados; lóbulos del cáliz caducos en el fruto joven; corola no azul con lóbulos lineares monomórficos, el par dorsal extendido o recurvado horizontalmente, desde tan largo como el tubo rígido hasta tres veces más largo, el ventral connado en $\frac{2}{3}$ de su longitud o más, formando un labio trifido reflejo y enrollado más corto que el par dorsal; columna estaminal exerta, las cinco anteras con penachos apicales de tricomas blancos; cápsula apicalmente loculicida cubierta en la madurez por una red irregular de haces esclerenquimáticos; y semillas oblongas aladas con una testa débilmente estriada. La sección es endémica de las Islas Hawai, con dos especies en cada una de las Kaua'i (*L. villosa* y ***L. wahiawa***, sp. nov.) y O'ahu (*L. gaudichaudii* y ***L. koolauensis***, comb. et stat. nov.), y una sola especie (*L. gloria-montis*) en Maui y Moloka'i, dividida en dos subespecies: subsp. *gloria-montis* (West Maui and Moloka'i) y subsp. ***longibracteata***, stat. nov. (West Maui y East Maui). Las dos especies de Kaua'i hibridan produciendo ***L. xkauaiensis***, stat. nov.

The finest of our lobelias is Lobelia gloria-montis, a truly royal and superb plant ...

To see this species growing is one of the delights of the botanist.—Rock (1919: 35, 117)

The Hawaiian archipelago is renowned among botanists for the many compositional peculiarities of its flora (MacCaughey 1917; Hitchcock 1919; Carlquist 1974, 1980; Wagner et al. 1990). Among the most peculiar is the fact that the family with the greatest number of native species is not Gramineae Juss. or Compositae Giseke, but Campanulaceae Juss.; at no other spot on the globe does this family predominate statistically. In a flora of not quite 1000 indigenous species (Wagner et al. 1990), 134 of them (all endemic) belong to Campanulaceae (Lammers 2007a). Furthermore, these 134 species represent nearly 6% of all species in this cosmopolitan family, although the Hawaiian Islands only comprise 0.004% of Earth's land surface. Six genera are present, all members of subfamily Lobelioideae Burnett. Five are endemic and assigned to the tribe Delisseae C. Presl: *Brighamia* A. Gray, *Clermontia* Gaudich., *Cyanea* Gaudich., *Delissea* Gaudich., and *Trematolobelia* Zahlbr. ex Rock. The only one of the six not endemic to the archipelago is *Lobelia* L., a member of tribe Lobelieae Rchb., which is virtually cosmopolitan in its distribution.

Lobelia is the largest of the 29 genera in the Lobelioideae, comprising 405 species of annual and perennial herbs, shrubs, and trees (Lammers 2007a). The genus is characterized by solitary or racemose flowers on usually bibracteolate pedicels; corollas with the tube dorsally cleft to the base and the lobes monomorphic,

or dimorphic and the ventral larger; and apically bivalvate capsules or rarely berries (Murata 1995; Lammers 2004a, 2007b).

Because of its large number of species, *Lobelia* has been divided into a number of sections and other infrageneric taxa over the years. The first species described from the Hawaiian Islands, *L. gaudichaudii*, was assigned to sect. *Homochilus* A. DC. by Candolle (1839). As additional Hawaiian species of *Lobelia* were discovered during the Nineteenth Century, they all were assumed to be related to *L. gaudichaudii*. Benth (1876) removed these Hawaiian species from sect. *Homochilus* to sect. *Rhynchopetalum* (Fresen.) Benth. (cf., Lammers 2004b); the latter subsequently was subsumed into sect. *Tylomium* (C. Presl) Benth. by Schönland (1889).

In contrast to this single-taxon view of Hawaiian *Lobelia*, Rock (1919) believed that the Hawaiian species of *Lobelia* actually formed two taxa that were not each other's closest relatives: (1) *L. gaudichaudii* and allied species, characterized by a large white, yellow, red, or purple-striped corolla with stout tube and spreading or horizontally recurved dorsal lobes, and all five anthers apically tufted; and (2) *L. yuccoides* Hillebr. and allied species, characterized by a small blue or magenta corolla with slender tube and recoiled dorsal lobes, and only the ventral pair of anthers apically tufted. This two-taxon hypothesis was supported by Skottsberg (1928) and Carlquist (1980), and formalized by Wimmer (1948), who erected two sections within *Lobelia* subg. *Tupa* (G. Don) E. Wimm. to accommodate the Hawaiian endemics: sect. *Galeatella* E. Wimm. for *L. gaudichaudii* and its allies, and sect. *Revolutella* E. Wimm. for *L. yuccoides* Hillebr. and its allies (Wimmer 1953, 1968). Although Mabberley (1974, 1975) suggested returning both groups to different parts of sect. *Rhynchopetalum*, he did not effect these changes and Wimmer's arrangement is the classification in current use (Lammers 1990, 2007a, 2007b; Murata 1995).

Over the past 15 years, the summary of Hawaiian Campanulaceae that I prepared (Lammers 1990) for the *Manual of the flowering plants of Hawai'i* (Wagner et al. 1990) has been expanded into a series of monographs. Previous entries covered *Brighamia* (Lammers 1989), *Clermontia* (Lammers 1991), and *Delissea* (Lammers 2005). The present effort covers *Lobelia* sect. *Galeatella*. This treatment will also form part of a series of monographs of the sections of *Lobelia* subg. *Tupa*; previous entries in that series accounted for sect. *Tupa* (G. Don) Benth. (Lammers 2000) and sect. *Homochilus* (Lammers 2004b).

TAXONOMIC HISTORY

As might be expected from their predominance in the Hawaiian flora, Lobelioideae were among the first botanical specimens collected in the islands at the time of their discovery by Europeans in 1778 (St. John 1977a, 1977b, 1979). However, it was another half century before botanists visiting the archipelago obtained specimens referable to *Lobelia* sect. *Galeatella*. During an October 1836 visit to O'ahu by the French corvette *La Bonite* (cf., Lasègue 1845; Kuykendall 1947), ship's naturalist Charles Gaudichaud-Beaupré reached the summit of the Ko'olau Range above Honolulu harbor (St. John & Titcomb 1983). Here he collected a pachycaul species of *Lobelia* a meter tall with a thick pithy stem densely covered in transversely rhombic leaf scars, a dense apical rosette of coriaceous leaves, a terminal raceme of large red flowers, and capsules filled with flat winged seeds. Not long after, Swiss botanist Alphonse de Candolle saw the specimen in the herbarium at Paris and named it in Gaudichaud's honor (Candolle 1839). Although Gaudichaud never published a description of *Lobelia gaudichaudii* himself, the atlas of *La Bonite's* voyage (Gaudichaud s.d.) did include an illustration, labeled with Candolle's binomial; the fascicle of the book containing this plate is believed to have appeared in 1842 (Stafleu & Cowan 1976).

The United States Exploring Expedition (cf., Wilkes 1845; Jackson 1985) called at the Hawaiian Islands during 1840–41 and collected specimens of *Lobelia* on Kaua'i that were very similar to *L. gaudichaudii* of O'ahu. Harvard botanist Asa Gray (cf., Dupree 1959; St. John 1985) segregated these plants from the species as *L. gaudichaudii* var. *kauaiensis* (Gray 1861; Mann 1867). However, Austrian botanist Heinrich Wawra, who visited the archipelago aboard the frigate *Donau* during 1869–70, did not distinguish the specimens he had gathered on O'ahu and Kaua'i, calling them all *L. gaudichaudii* (Wawra 1873). This single-taxon approach

was also adopted by the islands' first resident botanist, Wilhelm Hillebrand (cf., Degener 1957; Lammers 1994), who broadened the circumscription of the species even further by including plants he had discovered on West Maui (Hillebrand 1888).

American Amos Arthur Heller, who botanized on O'ahu and Kaua'i in 1895 (cf., Wagner & Shannon 1999), not only disagreed with this single-taxon view, but further disagreed with their original treatment as conspecific varieties. He segregated the Kaua'i populations from *L. gaudichaudii* as *L. kauaiensis*, commenting (Heller 1897: 911), "Had Dr. Gray seen [plants of O'ahu and Kaua'i] in the living state, he certainly would not have considered the one a mere form of the other, worthy of varietal rank only."

The next botanist to deal with these plants was Austrian expatriate Joseph Rock, who resided in the islands from 1907 to 1920 and again from 1953 until his death in 1962 (cf., Chock 1963; Sutton 1974). At first, he accepted Heller's two-species treatment, but modified it slightly by describing three new varieties. Thinking that the white-flowered plants on West Maui were the original nomenclatural type of *L. gaudichaudii*, he segregated the red-flowered O'ahu populations as *L. gaudichaudii* var. *coccinea* (Rock 1917); only later did he realize that this was an error and that the type of the species was actually a red-flowered plant from O'ahu. Tall plants with very long floral bracts and calyx lobes that he discovered on West Maui were distinguished as *L. gaudichaudii* var. *longibracteata* (Rock 1913a, 1913b), while plants with densely pubescent inflorescences that he discovered on Kaua'i were segregated as *L. kauaiensis* var. *villosa* (Rock 1917). However, in his subsequent monograph of the Hawaiian *Lobelioideae* (Rock 1919), he treated the plants of each island as a discrete species: *L. kauaiensis* and its var. *villosa* on Kaua'i, *L. gaudichaudii* (with var. *coccinea* in synonymy) on O'ahu; and the newly described *L. gloria-montis* and its var. *longibracteata* on West Maui.

When plants referable to sect. *Galeatella* were found on Moloka'i, Degener (1938a) named them *L. gloria-montis* var. *molokaiensis*, though a paucity of good material precluded an adequate description. Similarly, when white-flowered plants with a branched inflorescence was discovered in the northwestern Ko'olau Range, Fosberg and Hosaka (1938) described them as a variety of the O'ahu species, *L. gaudichaudii* var. *koolauensis*.

The first dedicated taxonomic study of these plants was by University of Hawaii professor Harold St. John (cf., Anonymous 1980, 1991) and his student Edward Hosaka. Their revision (St. John & Hosaka 1938) resurrected Hillebrand's (1888) broad circumscription of *L. gaudichaudii*, including in it plants of O'ahu, Kaua'i, and West Maui. Within this broad circumscription, they distinguished five geographic varieties: var. *gaudichaudii* (as "var. *typica*" and including var. *coccinea* as a synonym), var. *gloria-montis* (with three heterotypic *formae*), var. *kauaiensis* (with one heterotypic *forma*), var. *koolauensis*, and var. *longibracteata*; var. *molokaiensis* was excluded for want of adequate material. However, not all Kaua'i plants were included in *L. gaudichaudii* var. *kauaiensis*; those recognized previously as *L. kauaiensis* var. *villosa* were accorded specific rank as *L. villosa*. Years later, a population discovered on East Maui was described (St. John & Medeiros 1987) as a sixth geographical variety, *L. gaudichaudii* var. *albiflora*.

When Viennese botanist Franz Elfried Wimmer (cf., Rechinger 1961; Degener & Degener 1962a) prepared his monograph of *Lobelia* for *Das Pflanzenreich* (Wimmer 1953), his treatment of sect. *Galeatella* was identical to that of St. John and Hosaka (1938). In subsequent years, however, his view of the group changed. In a letter to Otto Degener dated 20 November 1958 (quoted by Degener & Degener 1974), he indicated his intention to accord the group generic status under the name "Schiexelia," and to recognize five species therein. His posthumously published supplement to the *Pflanzenreich* monograph (Wimmer 1968) did recognize five species: *L. kauaiensis* and *L. villosa* on Kaua'i, *L. gaudichaudii* on O'ahu; and *L. gloria-montis* and *L. longibracteata* (newly elevated from varietal rank) on West Maui. However, no mention was made of elevating the section to generic rank and it remained a section of *Lobelia* subg. *Tupa*. Degener and Degener (1962b, 1974, 1983) carried through on the elevation to generic rank, though they disregarded Wimmer's provisional name and took up the sectional epithet at the new rank. Their synopsis of the group (Degener & Degener 1974) maintained Wimmer's (1968) five-species classification. My treatment in the *Manual* (Lammers 1990) was essentially the same, except for including *L. longibracteata* within *L. gloria-montis*.

MATERIALS AND METHODS

Revision of the classification of *Lobelia* sect. *Galeatella* was based upon morphological data; definitions of qualitative character states follow Harris and Harris (1994). These data were gathered from almost 300 specimens (including the types of all heterotypic names) deposited in 31 herbaria (see Acknowledgments for a complete list).

The data obtained from these specimens were analyzed via traditional taxonomic methodology (Leenhouts 1968; Qualls 1986; Vogel 1987; Maxted 1992; Watson 1997; Winston 1999) within a geographic framework. Populations referable to sect. *Galeatella* are known from just six discrete areas on four islands: (1) the Wahiawa drainage of south-central Kaua'i at 570–800 m; (2) the Alaka'i Swamp of north-central Kaua'i, from Pihea to Wai'ale'ale, at 1100–1590 m; (3) the Ko'olau Range of O'ahu, from Pu'u Ka'inapua'a to Mt. Olympus, at 670–960 m; (4) the mountains of West Maui at 915–1760 m; (5) the northwestern slopes of Haleakalā on East Maui at 1280–1700 m; and (6) eastern Moloka'i from Pāpa'alā to Kalua'aha at 1165–1350 m. Because of the extreme precinctiveness of the Hawaiian flora (MacCaughey 1917; Hitchcock 1919; Carlquist 1980; Wagner et al. 1990), I hypothesized that each of these six areas would harbor a single taxon unique to that locale, or at least to that island. Therefore, when inspecting the data, I asked two questions. First, were all specimens from a given area relatively homogeneous, with most characters evincing a continuous pattern of variation? If so, the hypothesis would be supported; if instead, several characters consistently showed correlated gaps in their patterns of variation within an area, the hypothesis would be refuted. Second, are the plants that evince a given correlated suite of morphological features restricted to a single area or island? If so, the hypothesis would be supported; if not, the hypothesis would be refuted.

Once taxa had been discerned in this fashion, they were compared to nomenclatural type specimens to determine the correct name under the *International Code of Botanical Nomenclature* (ICBN; McNeill et al. 2006). Decisions on rank for the taxa were made in light of the definitions of species and subspecies that I have employed previously (Lammers 1991, 2007a).

RESULTS AND DISCUSSION

In revising *Lobelia* sect. *Galeatella*, three aspects of its classification were evaluated in light of the assembled data: (1) the circumscription of the group, (2) its position and rank, and (3) its division into component taxa.

Circumscription.—The circumscription and characterization of *Lobelia* sect. *Galeatella* have been invariant since its publication by Wimmer (1948). Overall similarity among populations is quite high; recall that the entire section has been treated as just one or two species until recently, with most variation expressed by distinguishing geographic varieties. Furthermore, much of this overall similarity involves characters that are quite unusual among Lobelioideae.

Most species of *Lobelia* are hemicryptophytes or therophytes (Lammers 2007a); woodiness is less common, confined to certain groups within subg. *Tupa* (Carlquist 1969; Murata 1995). Even among those species that are woody, the growth form of sect. *Galeatella* is unusual. In sect. *Tylomium* (Wilbur 1991), sect. *Tupa* (Lammers 2000), and sect. *Homochilus* (Lammers 2004b), the woody species are iteroparous (polycarpic) shrubs with several leptocaul stems that persist, branch, and flower each growing season. In sect. *Galeatella*, in contrast, the stem is pachycaul, unbranched, pliestesial (i.e., requiring several to many years of growth before it achieves sufficient mass to flower), and hapaxanthic (i.e., dying after flowering). Although Truman and Augspurger (1991) described these species as semelparous (monocarpic), this is incorrect. An individual shoot does indeed die by the time the capsules dehisce and disperse ripe seed. However, a new shoot emerges around the base of the plant (presumably from a root bud) to replace it. This sucker, which is far more pubescent than a mature shoot (cf., the “juvenile plant” of Degener 1938a), will eventually grow into a new flowering shoot (Hillebrand 1888; pers. observ.). As such, the individual plant is in fact iteroparous (polycarpic), conforming to the “Tomlinson” architectural model (cf., Hallé & Oldeman 1970; Hallé et al. 1978).

Similarly, the winged seeds of sect. *Galeatella* (Fig. 1) are unusual in *Lobelia*, occurring elsewhere only in some species of sect. *Rhynchoptalum* and sect. *Trimeris* (C. Presl) A. DC. [the earliest available name for sect. *Colensoa* (Hook. f.) J. Murata] (Mabberley 1975; Murata 1995; Buss et al. 2001). The possession of apical tufts of trichomes on all five anthers rather than just the ventral pair is otherwise unknown in subg. *Tupa*, though it does characterize sect. *Cryptostemon* (E. Wimm.) J. Murata and sect. *Delostemon* (E. Wimm.) J. Murata in herbaceous subg. *Lobelia* (Murata 1995).

In summary, the assemblage of morphological features that characterize these Hawaiian species is found in no other species of Lobelioideae and the circumscription adopted here is confidently believed to create a natural group.

Position and rank.—In contrast to circumscription, there has been a diversity of opinion regarding the relationships of *Lobelia* sect. *Galeatella* to other taxa of Lobelioideae and the appropriate rank at which to recognize the taxon. Most authors who have commented on relationships agree in identifying as the group's closest relatives certain species assigned to another section in *Lobelia* subg. *Tupa*, sect. *Trimeris*. However, they disagree on specifics. Rock (1919) allied the group to tropical Asian members of the group, such as *L. boninensis* Koidz. and *L. pyramidalis* Wall., while Mabberley (1974, 1975) saw a relationship to Brazilian species such as *L. hassleri* Zahlbr. and *L. organensis* Gardner. The endemic Hawaiian genus *Trematolobelia* has also been suggested as a close relative by some (Candolle 1839; Stapf 1893; Mabberley 1975). As for rank, the group has been treated as either a section within *Lobelia* subg. *Tupa* (Wimmer 1948, 1953, 1968; Lammers 1990, 2007b; Murata 1995) or as a genus distinct from *Lobelia* (Degener & Degener 1962b, 1974, 1983).

Because of the geological youth and *de novo* volcanic origin of the Hawaiian Islands, it is assumed that its flora developed from continental species that in some way were able to colonize the archipelago via long-distance dispersal (Guppy 1906; Brown 1921; Carlquist 1974; Funk & Wagner 1995). For many years, it was hypothesized that multiple colonizations were required to explain the 134 endemic species of Lobelioideae: a common one for *Clermontia*, *Cyanea*, and *Delissea*, and separate ones for each of the remaining taxa, including *Lobelia* sect. *Galeatella* (Rock 1919; Stone 1967; Carlquist 1980; Mabberley 1974, 1975; Lammers 1990).

However, recent analyses of molecular data (Knox et al. 1993; Givnish et al. 1995; E. Knox, Indiana University, pers. comm.; A. Antonelli, Göteborg University, pers. comm.) have dealt a devastating blow to this polyphyletic hypothesis. All these studies indicate that the endemic Hawaiian Lobelioideae are monophyletic, i.e., that all 134 species in six genera evolved from a single ancestral colonization of the archipelago. The Hawaiian species (as well as *Apetahia* Baill. and *Sclerotheca* A. DC., genera endemic to islands of the southwestern Pacific) form a well supported clade in these analyses. Its sister-group is a clade comprising the African and Brazilian species of sect. *Rhynchoptalum* and sect. *Trimeris*, and the outgroup of this larger Hawaiian-African-Brazilian clade is a group of tropical Asian species of sect. *Trimeris*. Consequently, the species that Rock (1919) and Mabberley (1974, 1975) believed were the immediate ancestors of sect. *Galeatella* are more distantly related, and the group's closest relatives actually are to be found among the Hawaiian endemics.

The molecular analyses cited above indicate that the Hawaiian clade comprises two subordinate clades: one comprising the genera with axillary inflorescences (*Brighamia*, *Clermontia*, *Cyanea*, *Delissea*) or solitary axillary flowers (*Apetahia*, *Sclerotheca*) and the other comprising the taxa with terminal inflorescences (*Lobelia* sect. *Galeatella*, *Lobelia* sect. *Revolutella*, and *Trematolobelia*). Within the latter subclade, sect. *Galeatella* is sister to *Trematolobelia* while sect. *Revolutella* is their outgroup.

The sister-group relationship between sect. *Galeatella* and *Trematolobelia* is supported by morphology. Overall, the two are very similar in structure and appearance. Both are pachycaul treelets with a solitary pliestesial hapaxanthic shoot; a dense apical rosette of coriaceous leaves leaving a helical pattern of raised corky cicatrices on the unbranched stem; a terminal bracteate raceme of large ornithophilous flowers; calyx lobes caducous from the young fruit; non-blue corolla with linear monomorphic lobes; and exerted staminal

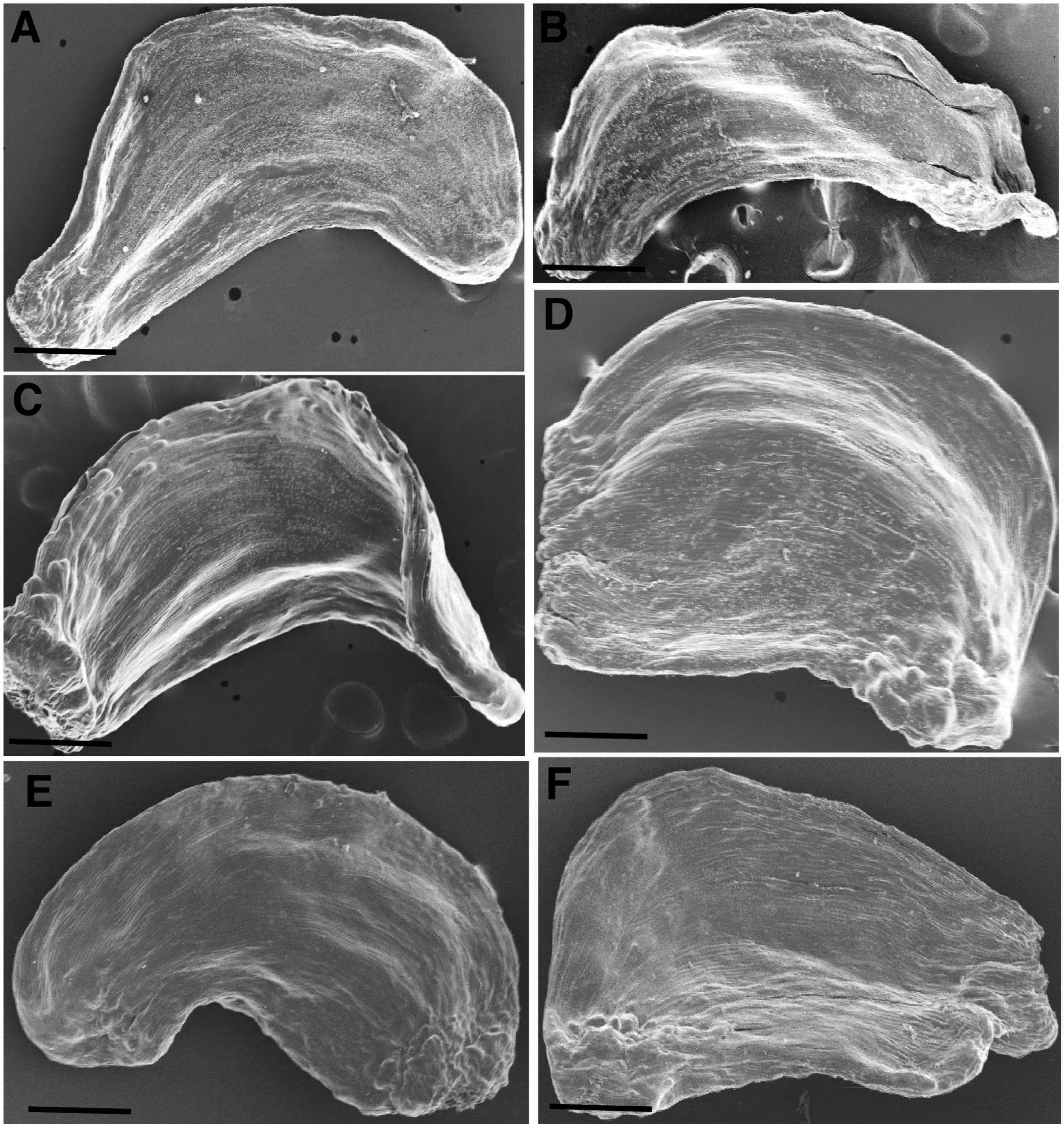


FIG. 1. Seeds of *Lobelia* sect. *Galeatella*, prepared following Buss et al. (2001). Scale bars = 625 μm . A. *L. villosa* (Flynn 685, PTBG). B. *L. xkauaiensis* (Hitchcock 15437, US). C. *L. wahiawa* (Forbes 294, K, US). D. *L. koolauensis* (Fosberg 14224, K). E. *L. gaudichaudii* (Garber 82, BISH). F. *L. gloria-montis* subsp. *gloria-montis* (Hitchcock 14735, US).

column. Both groups also have relatively large winged seeds and an irregular network of sclerenchymatous bundles in the pericarp, character states unusual among *Lobelioideae*, which may serve as synapomorphies uniting them.

In attempting to distinguish *Lobelia* sect. *Galeatella* from *Trematolobelia*, I could identify just five morphological characters that were consistently useful. Using the horizontal posture of the inflorescence branches as a distinguishing character for *Trematolobelia* is compromised by the erect unbranched inflorescence of *T. singularis* H. St. John; cf., Carlquist 1980, pg. 212D [top]. Similarly, use of corolla color is precluded by overlap; red and white flowers are found in species of both groups.

Although both taxa are characterized by a woody stem that is pachycaul, unbranched, pliestesial, and hapaxanthic, there is a fundamental difference in longevity. While individual plants of sect. *Galeatella* are iteroparous (polycarpic) via basal offshoots (the “Tomlinson” architectural model), individuals of *Trematolobelia* are semelparous (monocarpic), dying by the time the capsules dehisce and disperse ripe seed (the “Holttum” architectural model; Hallé & Oldeman 1970; Hallé et al. 1978). The latter plan may have evolved from the former through the simple suppression of the basal offshoots.

Lobelia sect. *Galeatella* further differs from *Trematolobelia*, and is unusual among species of *Lobelia* subg. *Tupa*, in having ebracteolate (vs. bibracteolate) pedicels and all five anthers (vs. just the ventral pair) bearded at the apex with tufts of stiff white trichomes; these two characters are potential synapomorphies for the species of sect. *Galeatella*. Conversely, *Trematolobelia* differs from sect. *Galeatella* and is unique among Lobelioideae in its strongly secund (vs. ample) inflorescences and laterally poricidal (vs. apically loculicidal) capsule; these characters are potential synapomorphies for the species of *Trematolobelia*.

Although the fruit of *Trematolobelia* (described in detail by Carlquist 1962) is unique in the subfamily, there is some similarity to the fruit of sect. *Galeatella*, as noted by Hillebrand (1888) and Stapf (1893). In all Lobelioideae, the ovary is adnate to a hypanthium of appendicular origin (Kaplan 1967). As a result, the pericarp of the fruit is actually a combination of hypanthial and gynoecial tissue. In both *Trematolobelia* and sect. *Galeatella*, the calyx lobes are caducous early on; the exocarp and the parenchymatous portions of the mesocarp deliquesce and are washed away by the frequent rains, leaving behind a series of sclerenchymatous bundles surrounding the endocarp. In sect. *Galeatella*, this mesocarpal network is open distally, forming an open basket or cup. The endocarp it loosely encloses is thick and woody, and dehisces apically through a pair of triangular loculicidal valves. In *Trematolobelia* in contrast, this mesocarpal network anastomoses distally, forming a laterally foraminate sphere. The endocarp is tightly enclosed and adnate to the sclerenchymatous mesocarp at its summit, precluding the formation of dehiscent valves. Instead, the wall is thin and papery, rupturing irregularly at its base. This releases the seeds, which accumulate in the bottom of the mesocarpal network. When the plant is flailed by the strong winds characteristic of its montane habitat, the winged seeds are shaken out through the lateral foramina in the sclerenchymatous mesocarp.

These similarities suggest that the fruit of sect. *Galeatella* represents an intermediate step in the evolution of the unique poricidal capsule of *Trematolobelia* from the loculicidal capsules with intact exocarp and mesocarp that are more typical of the Lobelioideae. All of the necessary components are in place: the caducous calyx lobes, the mesocarpal bundles, the deliquescent exocarp and mesocarp parenchyma, and the winged seeds. All that was required was (1) the apical closure and contraction of the mesocarpal network, (2) cessation of apical dehiscence via adnation of the endocarp to the mesocarpal sclerenchyma, and (3) the thinning of the endocarp.

In light of the well supported phylogenetic relationship between sect. *Galeatella* and *Trematolobelia*, the current classification at these ranks appears suboptimal. From a cladistic perspective, sister-groups should have the same rank. This could be achieved in the present case by elevating sect. *Galeatella* to generic rank, following Degener and Degener (1962b, 1974, 1983); by including *Trematolobelia* in *Lobelia* as another section, following Post and Kuntze (1903); or by expanding *Trematolobelia* to encompass sect. *Galeatella*.

However, I have elected to do none of these at present but rather to maintain the *status quo* and continue *pro tempore* to treat this taxon as a section within *Lobelia* subg. *Tupa*. First, it seems best to complete projected studies of sect. *Revolutella* and *Trematolobelia* before making changes in the position and rank of sect. *Galeatella*. These three taxa are intimately connected and any necessary changes would best be made in concert. Second, the molecular analyses cited above raise issues that extend beyond far beyond the Hawaiian Islands. The sampled species of *Lobelia* in these studies fall throughout the phylogeny of the subfamily, from the very first branch to the last; all other genera sampled thus far are embedded among them. Thus, as currently circumscribed, *Lobelia* is one of the most unnatural genera imaginable. It not only violates key principles of cladistic classification, but of traditional taxonomy as well. If we are to avoid treating the entire subfamily as a single genus comprising 1192 species (Lammers 2007a), it will be necessary to segregate

a number of genera from *Lobelia*. However, the studies cited above have not yet reached the point where it is feasible to do so. Although the overall problem is obvious, the best resolution is not yet evident. Any changes in the position and rank of the Hawaiian taxa of *Lobelia* would best be done as part of the overall realignment of the genus.

Component taxa.—My original hypothesis, that each of the six areas in which sect. *Galeatella* occurs would possess a taxon unique to that locale, was not supported. Analyses of the data revealed a total of seven taxa. Half the sites harbored two or even three taxa, and only four of the seven taxa were confined to a single site. On the other hand, all taxa but one were confined to a single island, and even that one exception may prove to be spurious once additional specimens have been studied.

The specimens examined from the Alaka'i Swamp of north-central Kaua'i formed three groups on the basis of morphology. The most widely distributed, occurring throughout the length of the region from Pihea to Wai'ale'ale, is also the most distinctive member of the entire section, differing from all others by its densely pubescent inflorescence on a conspicuously bracteate peduncle, pale yellow flowers that are the smallest in the section, floral bracts rounded or subcordate at base, and calyx lobes rounded or obtuse at apex. The type of *L. kauaiensis* var. *villosa* is a representative of this taxon.

At the southeastern terminus of the Alaka'i Swamp, on the summit of Wai'ale'ale, are found plants that differ considerably from the last. This taxon is characterized by depressed obtrullate or depressed obovate cicatrices on the stems, linear or oblanceolate leaves, a tall (1.5–2.5 m) glabrous branched inflorescence with blackish purple axes and a largely naked peduncle, relatively narrow floral bracts, relatively large flowers, calyx lobes acute or acuminate at apex, a pale purple corolla with dark purple longitudinal veins, and large (1.7–2.5 mm long) seeds. This glabrous taxon corresponds to St. John and Hosaka's (1938) concept of *L. gaudichaudii* var. *kauaiensis*; however, as pointed out by Skottsberg (1944), it does not match the type of that name: the inflorescence in the type specimen is somewhat pubescent, while the apex of the calyx lobes is rounded. In fact, none of the type specimens referable to sect. *Galeatella* match these plants, meaning that none of the available names apply to the taxon; though known for well over a century, it has no name.

The third taxon is likewise found on Wai'ale'ale, but also has been collected at the opposite end of Alaka'i Swamp, at Pihea. It resembles the unnamed glabrous taxon in its depressed obtrullate or depressed obovate cicatrices on the stems, linear or oblanceolate leaves, branched inflorescence, relatively large flowers, longitudinally striped pale purple corolla, and relatively large (2–3 mm long) seeds. However, it differs in its somewhat pubescent inflorescence with green axes, broader floral bracts, rounded calyx lobes, and pink corolla venation; the inflorescence is also shorter on average (1–2 m). The types of *L. gaudichaudii* f. *hirsuta* and *L. gaudichaudii* var. *kauaiensis* represent this taxon.

As noted above, the densely pubescent taxon that corresponds to the type of *L. kauaiensis* var. *villosa* is found throughout the Alaka'i Swamp and is the most distinctive member of the section. The totally glabrous taxon occurs at just one place within its range, and at that place, the somewhat pubescent taxon is also found. The densely pubescent taxon and the glabrous taxon exhibit pronounced differences in flower color and size. Especially noteworthy is the gap in the lengths of their staminal columns: 45–57 mm long in the densely pubescent plants vs. 70–80 mm long in the glabrous ones. All this suggests that they are isolated reproductively under normal circumstances and merit distinction at specific rank. The name *L. villosa* is available for the densely pubescent species; the glabrous species is christened *L. wahiawa* below.

The somewhat pubescent plants at Pihea and Wai'ale'ale resemble *L. wahiawa* in several characters, as noted above; the characters by which they differ may be interpreted as due to the genetic influence of *L. villosa*. The inflorescence is shorter, more pubescent, and not darkly pigmented; the floral bracts are wider and the calyx lobes more rounded; and the pigmentation of the corolla veins is diluted. For these reasons, this taxon is here interpreted as an interspecific hybrid between *L. villosa* and *L. wahiawa*. It is this taxon to which the name *L. kauaiensis* properly applies. I generally have not endorsed the practice of christening occasional interpecific hybrids with binomials. In this case, however, retaining a well known name in a new status may result in less confusion than if it simply disappeared. Therefore, *L. villosa* × *L. wahiawa*, which has

been called *L. gaudichaudii* var. *kauaiensis* f. *hirsuta* (St. John & Hosaka 1938; Wimmer 1953) or *Galeatella kauaiensis* var. *hirsuta* (Degener & Degener 1962b, 1974), now will be called *L. ×kauaiensis*.

In the Wahiawa drainage of south-central Kaua'i, only a single taxon is found and it is *L. wahiawa*. Thus, the range of this species is largely allopatric from *L. villosa*. The latter is confined to the high elevations of the Alaka'i Swamp while *L. wahiawa* occurs in the low elevations of Wahiawa Swamp, except for the single population in the Alaka'i Swamp at Wai'ale'ale. It is possible that the sympatry of the two on Wai'ale'ale is a relatively recent phenomenon: the winged seeds of lowland *L. wahiawa* may have been carried the 10 km to the mountaintop and successfully established there. Hybridization then occurred from time to time. The presence of the hybrid without *L. wahiawa* at Pihea (15 km northwest of Wai'ale'ale) could be explained by the dispersal of pollen of the absent parent via nectarivorous bird (cf., Lammers & Freeman 1986; Lammers et al. 1988) or by dispersal of hybrid seed from Wai'ale'ale. It could also be evidence of a second montane colonization, as yet undocumented or now extirpated, by *L. wahiawa*.

The specimens examined from O'ahu differ from all others in the section by their relatively short (0.4–1 m) cylindrical inflorescences, distinctly revolute leaves typically pubescent on the abaxial midrib, and small (1–1.8 mm long) seeds. Other characters, however, vary among these specimens; furthermore, this variation is correlated with geography. Specimens from the northwestern portion of the Ko'olau Range, between Pu'u Ka'inapua'a and 'Eleao at elevations of 670–860 m, are characterized by a 2–6-branched inflorescence, white corolla, dorsal anthers 14–16 mm long, capsules 18–21 mm long and 9–10 mm in diameter, and seeds 1.5–1.8 mm long; the type of *L. gaudichaudii* var. *koolauensis* represents this taxon. Specimens from the southeastern Ko'olau Range, between Pu'u Pauao and Mt. Olympus at 825–960 m, differ by their usually unbranched inflorescence, red corolla, shorter (10–13 mm) dorsal anthers, larger (23–30 × 11–10 mm) capsules, and smaller (1–1.5 mm) seeds; the types of *L. gaudichaudii* and *L. gaudichaudii* var. *coccinea* are representatives of this taxon. Note that the ranges of these two taxa overlap between Pu'u Pauao and 'Eleao.

These two taxa were treated previously as conspecific and distinguished at either varietal (St. John & Hosaka 1938; Wimmer 1953, 1968; Degener & Degener 1962b, 1974) or subspecific (Lammers 1988, 1990) rank. However, as noted by St. John and Hosaka (1938), the northwestern Ko'olau plants seem almost as closely related to the plants of Kaua'i here called *L. wahiawa* as they do to the southeastern Ko'olau plants. Characters shared by that species and the northwestern Ko'olau plants (but not the southeastern) include the branched (vs. unbranched) inflorescence, light-colored (vs. red) corolla, dorsal anthers 14–16 (vs. 10–13) mm long, and seeds 1.5–2.5 (vs. 1–1.5) mm long.

While the unique characters shared by the O'ahu plants may suggest their derivation from a common ancestor, the characters that differ, particularly corolla color and anther length, are the sort that might be indicative of reproductive isolation. This hypothesis is supported by the absence of morphologically intermediate specimens in the zone of sympatry between Pu'u Pauao and 'Eleao. Because the evidence suggests that these two taxa are unable to interbreed in nature, they are accorded specific rank. The name *L. gaudichaudii* applies to the southeastern taxon, and the new combination *L. koolauensis* will be effected below for the northwestern one.

Specimens seen from West Maui share a distinctive suite of features that at once distinguishes them from the plants of Kaua'i and O'ahu: a pyramidal outline to the inflorescence, created by a progressive shortening of the pedicels from base to apex; lamina with a thickened or subrevolute margin typically ciliate toward base; the largest flowers and fruits in the group; and seeds of moderate size (2–2.3 mm long). Certain other characters, however, evince considerable variation.

In the majority of plants from West Maui (including the type specimens of *L. gaudichaudii* f. *kukuiensis* and *L. gloria-montis*), the inflorescence is glabrous and the corolla white. However, occasional specimens (such as the type of *L. gaudichaudii* f. *bryanii*) have a densely pubescent inflorescence, while in others (including the type of *L. gaudichaudii* f. *sanguinea*) the corolla is red. In neither case could I detect any correlation of the unusual character state with other morphological characters, or with geography, elevation, or habitat; the red-flowered variants at least are definitely reported to grow side-by-side with white-flowered plants

(Skottsberg 1944; Selling 1947). As such, it appears that each character—pubescent inflorescence and red corolla—is a simple genetic variant occurring sporadically within a population.

There are other specimens from West Maui that resemble the dominant morphotype in their glabrous inflorescence and white corolla, but that differ in other characters; furthermore, they are restricted to a different habitat. The plants mentioned in the preceding paragraph occur in open montane bogs on Pu‘u Kukui, ‘Eke, and other summits. All have a stem less than 1.5 m tall; an unbranched inflorescence; and relatively short floral bracts, pedicels, and calyx lobes. Specimens collected in forests at the head of ‘Īao Valley (cf., Rock 1913a, 1919) differ in their much taller (2.5–4 m) stems, 5–7-branched inflorescence, floral bracts 60–80 (vs. 20–47) mm long, pedicels 50–60 (vs. 15–45) mm long, and calyx lobes 30–35 (vs. 7.5–25) mm long. The type of *L. gaudichaudii* var. *longibracteata* is an example of these plants.

In my previous treatment (Lammers 1990), I did not distinguish these larger forest plants from the smaller bog plants at any rank, primarily because of the close proximity of their distributions. I certainly do not favor according them each specific rank as Wimmer (1968) and Degener and Degener (1974) have done. The characters that distinguish the two taxa are not the sort that might be expected to confer reproductive isolation, and in any case, evince some overlap in their ranges of values. As such, it is deemed best to treat them as conspecific ecological subspecies. The name for the species is *L. gloria-montis*. The small bog plants constitute autonymic subsp. *gloria-montis*, while the new combination subsp. *longibracteata* is effected below for the large forest plants.

Specimens from East Maui (including the type of *L. gaudichaudii* var. *albiflora*) are very similar to the tall forest plants of West Maui, with stem 2–4 m tall, floral bracts 62–65 mm long, pedicels 38–55 mm long, and calyx lobes 25–30 mm long; their habitat, described as forested margins of bogs, also seems quite similar. The only substantive difference is that the inflorescence of the East Maui plants, so far as known, does not branch. Given the small number of specimens representing the tall forest plants of East and West Maui, it seems best at present to assign them all to a single taxon. Consequently, the specimens from East Maui are here assigned to *L. gloria-montis* subsp. *longibracteata*.

The optimal disposition of the populations on Moloka‘i is uncertain. All known specimens (including the type of *L. gloria-montis* var. *molokaiensis*) are sterile. Although one would predict that a geographically isolated population might at least merit recognition at subspecific rank, the specimens at hand are indistinguishable from the typical morphotype of *L. gloria-montis* subsp. *gloria-montis*. Until more adequate material is available for study, these plants are assigned to that taxon.

In summary, sect. *Galeatella* is treated here as comprising five species. Kaua‘i and O‘ahu each have two endemic species: *L. villosa* and *L. wahiawa* on the former, *L. koolauensis* and *L. gaudichaudii* on the latter. The Kaua‘i pair hybridize where sympatric (*L. xkauaiensis*), while the O‘ahu pair do not. The fifth species (*L. gloria-montis*) is represented by two ecological races on West Maui: subsp. *gloria-montis* and subsp. *longibracteata*. The populations on East Maui and Moloka‘i are rather poorly known, but are assigned to *L. gloria-montis* subsp. *longibracteata* and *L. gloria-montis* subsp. *gloria-montis*, respectively.

TAXONOMIC TREATMENT

Lobelia sect. **Galeatella** E. Wimm., Ann. Naturhist. Mus. Wien 56:369. 1948. *Galeatella* (E. Wimm.) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE (designated by Degener & Degener 1962b): *L. kauaiensis* var. *villosa* Rock.

Pachycaul treelets of the “Tomlinson” architectural model (cf., Hallé & Oldeman 1970; Hallé et al. 1978), 0.7–5 m tall; plant polycarpic but the shoot pliestesial, hapaxanthic, and replaced by a sucker from the rootstock after fruit maturation. Stem 0.3–4 m tall, 0.8–10 cm diam., solitary and unbranched, erect or ascending, leafy only at apex; cicatrices raised, corky, transversely rhombic, depressed obtrullate, or depressed obovate in outline with a single central vein scar, closely packed in a helical pattern and long persistent; pith soft, broader than the lignified cortex toward apex but narrowing toward base as the cortex increases in thickness, becoming hollow with age; latex white, viscous. Leaves alternate, simple, exstipulate, sessile, glabrous or pubescent, forming a dense spherical or oblate apical rosette; lamina oblong, elliptic, lanceolate, oblanceolate, or linear, coriaceous, stiff, flat; margin entire, commonly revolute, with few to several intramarginal

callosities distally; apex acuminate, acute, or rarely obtuse; base attenuate or cuneate. Flowers tetracyclic, perfect, proterandrous, zygomorphic, epigynous, pedicellate, resupinate, ornithophilous, large; inflorescence an erect terminal pedunculate bracteate raceme, 0.4–2.5 m tall, unbranched or 2–7-branched from base, up to 100-flowered over its life, but seldom more than 4–8 open at any one time, glabrous or pubescent; peduncle usually shorter than rachis, densely to sparsely covered with reduced leaves (sterile bracts) that rapidly or gradually decrease in size acropetally; floral bracts conspicuous, equaling or shorter than the pedicels; pedicels ascending, stiff, ebracteolate. Calyx synsepalous, glabrous or pubescent; tube adnate to the basal $\frac{1}{3}$ – $\frac{2}{3}$ of the ovary, forming a broadly obconic (rarely campanulate or hemispherical) appendicular hypanthium $\frac{1}{5}$ – $\frac{1}{10}$ as long as the corolla; lobes 5, valvate, triangular, lanceolate, ovate, or oblong, shorter than the corolla tube, a little shorter than the hypanthium to over 4 times longer, the dorsal slightly longer than the ventral, caducous from the young fruit, the margin entire, the apex acuminate, acute, obtuse, or rounded and sometimes apiculate. Corolla sympetalous, zygomorphic, subbilabiate, of various colors (white, pale yellow, red, or pale purple with darker longitudinal veins) but never blue, glabrous (the lobes rarely pubescent at apex); tube straight or slightly curved, cylindrical or expanding slightly towards the mouth, 1.3–5 times longer than broad, dorsally cleft nearly to base but never fenestrate; lobes 5, valvate, linear, monomorphic, acuminate or acute at apex, the dorsal pair spreading or recurved horizontally, about as long as the tube to 3 times longer, the three ventral lobes connate for $\frac{2}{3}$ their length or more, forming a deflexed inrolled trifold lip shorter than the dorsal lobes. Stamens 5, antisealous, connate distally for most of their length, strongly exerted, emerging from the dorsal corolla slit above or between the dorsal lobes; filament tube suberect or slightly deflexed, 2.8–6.3 times longer than anther tube, glabrous (rarely short pubescent ventrally); dorsal anthers longer than the ventral, overhanging the orifice of the tube and somewhat occluding it; all 5 anthers with tufts of white trichomes at apex; pollen 52–54 μm polar diam. \times 35–41 μm equatorial diam., prolate, tricolporate, 3-celled at anthesis, the exine shallowly and minutely reticulate (Selling 1947; Erdtman 1952; Pandey et al. 1993). Ovary 2-loculed, inferior, adnate to the hypanthium for $\frac{1}{3}$ – $\frac{2}{3}$ its length, the conic apex free, forming a pronounced beak on the young fruit; placentae axile; ovules numerous; style 1, slender, terete, with a ring of stiff white hairs near the apex; stigma 2-lobed, the lobes appressed and non-receptive as the style grows through the anther tube, pushing out pollen, after which the stigmas spread and become receptive. Fruit an ovoid or ellipsoid capsule; exocarp and parenchymatous portions of the mesocarp deliquescent, leaving a loosely enshrouding series of sclerenchymatous bundles, open at top; endocarp rigid and durable, its conical apex splitting loculicidally into a pair of triangular valves; seeds (Fig. 1) winged, oblong, compressed, honey- or chestnut-brown, the narrow wing paler, the testa faintly striate (Type C of Murata 1992). Chromosome number unknown (Lammers 1993).

These species are restricted to wet habitats at elevations of 570–1760 m on four of the Hawaiian Islands. On Kaua'i and Maui, they are found in level saturated bogs, while on O'ahu and Moloka'i, they occur on windswept ridge crests and summit slopes. The plant communities that develop in all these areas (cf., Gagné & Cuddihy 1990) typically are dominated by dwarfed shrubs and various graminoids, and the species of *Lobelia* sect. *Galeatella* are typically among the tallest and most conspicuous elements in the vegetation (cf., Carlquist 1980, pp. 346, 350, 352 [bottom]). Flowering begins in mid-summer and is generally finished by October, with most seed maturing by January.

The flowers of these species, like most Hawaiian *Lobelioideae*, are presumed to be ornithophilous (Lammers & Freeman 1986; Lammers et al. 1988; Smith et al. 1995). Peale's (1848: 152) illustration of the endemic nectarivorous bird *Vestiaria coccinea* (Forster) of the Drepanidini (Aves: Fringillidae) includes an unequivocal depiction of *Lobelia gaudichaudii*; he commented that the bird's bill was "admirably adapted" for extracting nectar from its corolla. The flat winged seeds (Fig. 1) are presumably suited for a limited degree of anemochory.

Although none of the species has been examined cytologically, the group is hypothesized to be tetraploid with $2n = 28$, in light of the fact that all counted species of its sister-group (*Trematolobelia*) and their outgroup (*Lobelia* sect. *Revolutella*) have that number (Lammers 1993).

KEY TO THE SPECIES AND SUBSPECIES

1. Inflorescence densely pubescent, the peduncle densely covered with sterile bracts gradually decreasing in size acropetally, the floral bracts rounded or subcordate at base; hypanthium densely pubescent; calyx lobes obtuse or rounded at apex; corolla pale yellow, 44–57 mm long, the tube 1.3–2 times longer than broad, the ventral lip 22–24 mm long; filament tube 36–45 mm long; capsule 13–18 mm long (Alaka'i Swamp of Kaua'i) _____ **1. *Lobelia villosa***
1. Inflorescence glabrous (rarely pubescent), the peduncle sparsely covered with sterile bracts rapidly decreasing in size acropetally, the floral bracts cuneate at base; hypanthium glabrous (rarely pubescent); calyx lobes acuminate or acute (rarely rounded or obtuse) at apex; corolla pale purple with darker longitudinal veins, red, or white, 53–103 mm long, the tube 2–5 times longer than broad, the ventral lip 24–50 mm long; filament tube 57–80 mm long; capsule 19–37 mm long.
 2. Cicatrices depressed obtrullate or depressed obovate, the corners rounded; lamina 17–37 cm long, commonly linear; inflorescence 1–2.5 m tall; corolla pale purple with dark purple or pink longitudinal veins; seeds (1.7–)2–3 mm long (Kaua'i).
 3. Inflorescence 1–2 m tall, 13–35-flowered, its axis green and sparsely pubescent with relatively short curled trichomes; floral bracts elliptic, oblong, or obovate; calyx lobes rounded at apex; corolla with pink veins (Alaka'i Swamp) _____ **2. *Lobelia xkawaiiensis***
 3. Inflorescence 1.5–2.5 m tall, 20–85-flowered, its axis blackish purple and glabrous; floral bracts narrowly elliptic, narrowly oblong, or lanceolate; calyx lobes acuminate or acute (rarely obtuse) at apex; corolla with dark purple veins (Wahiawa & Alaka'i Swamps) _____ **3. *Lobelia wahiawa***
2. Cicatrices transversely rhombic, the corners acute; lamina 9–24 cm long, commonly oblanceolate; inflorescence 0.4–1.5 m tall; corolla red or white; seeds 1–2(–2.3) mm long.
 4. Inflorescence 0.4–1 m tall, cylindrical in outline; lamina distinctly revolute at margin, pubescence (if any) confined to abaxial midrib; corolla 58–78 mm long, the tube 19–31 mm long, the dorsal lobes 27–45 mm long; capsule 18–30 mm long; seeds 1–1.8 mm long (O'ahu).
 5. Inflorescence 2–7-branched; corolla white; dorsal anthers 14–16 mm long; capsule 18–21 mm long × 9–10 mm diameter; seeds 1.5–1.8 mm long (NW Ko'olau Range) _____ **4. *Lobelia koolauensis***
 5. Inflorescence unbranched; corolla red; dorsal anthers 10–13 mm long; capsule 23–30 mm long × 11–19 mm diameter; seeds 1–1.5 mm long (SE Ko'olau Range) _____ **5. *Lobelia gaudichaudii***
4. Inflorescence 1–1.5 m tall, pyramidal in outline; lamina subrevolute or merely thickened at margin, pubescence (if any) confined to basal margins; corolla 67–103 mm long, the tube 26–45 mm long, the dorsal lobes 35–70 mm long; capsule 27–37 mm long; seeds 2–2.3 mm long (Moloka'i, Maui) _____ **6. *Lobelia gloria-montis***
 6. Stems 0.4–1.5 m tall; floral bracts 20–47 mm long, obovate, elliptic, or lanceolate; pedicels 15–45 mm long; calyx lobes 7.5–25 mm long (Moloka'i, West Maui) _____ **6a. *Lobelia gloria-montis* subsp. *gloria-montis***
 6. Stems 2–4 m tall; floral bracts 60–90 mm long, oblong or linear; pedicels 38–60 mm long; calyx lobes 25–35 mm long (West and East Maui) _____ **6b. *Lobelia gloria-montis* subsp. *longibracteata***

1. *Lobelia villosa* (Rock) H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:124. 1938. *Lobelia kauaiensis* var. *villosa* Rock, Bull. Torrey Bot. Club 44:237. 1917. *Galeatella villosa* (Rock) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. KAUA'I: Wai'ale'ale, 21 Oct 1916, Rock 12844 (HOLOTYPE: BISH!; ISOTYPES: BISH! K!). The collection number is given as "12741" in the protologue and subsequent monograph (Rock 1919), but the figured specimen in the latter (pl. 61; called "Type" in the caption) shows this sheet with this number.

Plant 1.2–2.2 m tall. Stem 0.6–2 m tall × 1–6 cm diam.; cicatrices 3–3.5 mm tall × 6–7 mm wide, transversely rhombic, the corners acute. Lamina 14–22 cm long × 1.73 cm wide, oblong or oblanceolate, densely pubescent on margin, sometimes also pubescent on the dorsal and/or ventral midrib; margin subrevolute; apex obtuse or acute; base cuneate or attenuate. Inflorescence 0.5–1 m tall, 2–5-branched (rarely unbranched in small plants), densely pubescent, each branch 13–45-flowered and cylindrical in outline, its axis green; peduncle densely covered with sterile bracts that gradually decrease in size acropetally; sterile bracts 25–120 mm long × 10–30 mm wide, elliptic, oblong, lanceolate, ovate, or obovate, the apex acute or obtuse, the base rounded; floral bracts 17–30 mm long × 8–18 mm wide, elliptic, ovate or obovate, the apex acute or obtuse, the base rounded or subcordate; pedicels 15–35 mm long, of more-or-less equal length throughout. Hypanthium 5–9 mm long × 7–11 mm diam., broadly obconic, $\frac{1}{5}$ – $\frac{1}{10}$ as long as the corolla, densely pubescent; calyx lobes 8.5–12 mm long × 4–5 mm wide, triangular or oblong, equaling the hypanthium to 2.2 times as long, the apex obtuse or rounded. Corolla 44–57 mm long, pale yellow, glabrous; tube 15–18 mm long × 8–13 mm diam. at middle, straight, cylindrical or expanding slightly towards the mouth, 1.3–2 times longer

than broad; dorsal lobes 29–39 mm long \times 3.5–5 mm wide, 1.6–2.2 times longer than the tube; ventral lip 22–24 mm long \times 12–17 mm wide. Filament tube 36–45 mm long, slightly deflexed, 2.8–4.5 times longer than anther tube, glabrous; anther tube 4 mm diam.; dorsal anthers 9–13 mm long; ventral anthers 8–9.5 mm long. Capsule 13–18 mm long \times 10–12 mm diam.; seeds (Fig. 1A; Wimmer 1953, fig. 104c) 1.5–2.5 mm long \times 0.6–0.8 mm wide.

Icon.—Rock (1919), pl. 43. *Figured specimen.*—Rock (1919), pl. 61 [holotype].

Distribution, habitat, and phenology.—Endemic to north-central Kaua'i, known only from Montane Wet Mixed Communities (Gagné & Cuddihy 1990) of the Alaka'i Swamp (cf., Carlquist 1980, p. 350) from Pihea to Wai'ale'ale, at 1100–1560 m. Flowering from August to October. Considered “rare” by Wagner et al. (1999).

Representative specimens: **KAUAI. Waimea:** Alaka'i, bogs between Lehuamakanoe and Kilohana, *Cranwell et al.* 2984 (BISH, GB); Alaka'i Swamp, in 2nd large bog on trail to old USGS cabin on way to Wai'ale'ale, *Davis & Kores* 131 (BISH); Alaka'i Swamp, *Flynn* 685 (PTBG), *Flynn* 686 (PTBG); Alaka'i Swamp, *Forbes* 1122.K (BISH); Wai'ale'ale, *Hitchcock* 15450 (US); Alaka'i Swamp, along trail between Pihea and Kilohana, *Lammers et al.* 5376 (DUKE, F, OS); Wai'ale'ale, *Rock* 5823 *pro parte* (GH), *Rock* 8856 (BISH); Wai'ale'ale, 23 Sep 1909, *Rock s.n.* (BISH), Oct 1911, *Rock s.n.* (BISH); Alaka'i Swamp, *Yuncker* 3524 (DPU, US).

2. *Lobelia* \times *kauaiensis* (A. Gray) A. Heller, Minnesota Bot. Stud. 1:911. 1897 (as 'kauaensis', pro sp.) stat.

NOV. *Lobelia gaudichaudii* var. *kauaiensis* A. Gray, Proc. Amer. Acad. Arts 5:150. 1861 (as 'kauaensis'). *Galeatella kauaiensis* (A. Gray) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962 (as 'kauaensis'). TYPE: HAWAIIAN ISLANDS. KAUA'I: [Alaka'i Swamp, 30 Oct 1840, leg. W.D. Brackenridge & C. Pickering (*vide* Wilkes 1845),] *U.S. Exploring Expedition s.n.* (HOLOTYPE: US!; ISOTYPE: GH!). The epithet is based on the indeclinable Hawaiian proper noun “Kaua'i;” Gray's (1861) original spelling of the epithet is considered an orthographic error to be corrected, following Skottsberg (1944), Wimmer (1968), and Degener and Degener (1974).

Lobelia gaudichaudii f. *hirsuta* H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:121. 1938. *Galeatella kauaiensis* var. *hirsuta* (H. St. John & Hosaka) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. KAUA'I: Wai'ale'ale, Oct 1916, *Rock* 12845a (HOLOTYPE: BISH!; ISOTYPE: BISH!).

Plant 2.4–4 m tall. Stem 1–2 m tall \times 1–6 cm diam.; cicatrices 3–4.5 mm tall \times 4.5–8 mm wide, depressed obtrullate or depressed obovate, the corners rounded. Lamina 24–32 cm long \times 2.2–3.3 cm wide, linear, oblanceolate, or narrowly elliptic, glabrous or pubescent on ventral midrib; margin subrevolute; apex acuminate; base attenuate or cuneate. Inflorescence 1–2 m tall, 5-branched, sparsely pubescent with relatively short curled trichomes, each branch 13–35-flowered and cylindrical in outline, its axis green; peduncle sparsely covered with sterile bracts that rapidly decrease in size acropetally; sterile bracts 30–105 mm long \times 4–14 mm wide, linear or narrowly oblong, the apex acuminate, the base cuneate; floral bracts 12–23 mm long \times 4–10 mm wide, elliptic, oblong, or obovate, the apex obtuse or rounded, the base cuneate; pedicels 25–45 mm long, of more-or-less equal length throughout. Hypanthium 6–10 mm long \times 13–15 mm diam., broadly obconic, 1/7–1/11 as long as the corolla, glabrous or pubescent; calyx lobes 8–13 mm long \times 3–6 mm wide, triangular or oblong, equaling to a bit longer than the hypanthium, the margin entire, the apex rounded. Corolla 64–66 mm long, pale purple with pink longitudinal veins, glabrous; tube 20–22 mm long \times 10–12 mm diam. at middle, slightly curved, expanding slightly towards the mouth, twice as long as broad; dorsal lobes 42–46 mm long \times 4–5 mm wide, about twice as long as the tube; ventral lip 37–39 mm long \times 15–17 mm wide. Filament tube 64–66 mm long, suberect, 4 times longer than anther tube, glabrous; anther tube 4 mm diam.; dorsal anthers 14–16 mm long; ventral anthers 10–11 mm long. Capsule 19–30 mm long \times 8–20 mm diam.; seeds (Fig. 1B) 2–3 mm long \times 0.7–0.9 mm wide, chestnut-brown.

Icones.—Rock (1919), pl. 42 [right]; Wimmer (1968), fig. 29.

Distribution, habitat, and phenology.—A putative hybrid of *L. villosa* and the next species, known only from the Montane Wet Mixed Communities (Gagné & Cuddihy 1990) at the southeastern and northwestern extremities of the Alaka'i Swamp on north-central Kaua'i. At the former site (Wai'ale'ale, 1370–1570 m), it occurs with both parents, as evinced by *Rock* 5823; the sheet at BISH represents the hybrid, while that at GH is a mixed gathering of the two parents. At the latter site (Pihea, 1220–1350 m), *L. villosa* co-occurs but not the other parent. Flowering in August, fruit ripening in October. This taxon is listed as “rare” by Wagner et al. (1999), an assessment that also encompasses *L. wahiawa*.

Discussion.—Plants on Kaua'i that resemble the following species except for their puberulous raceme have been treated as a minor variant of it by most authors (Rock 1919; St. John & Hosaka 1938; Wimmer 1953; Degener & Degener 1962b, 1974). In my earlier treatment (Lammer 1990), I suggested that they were more likely interspecific hybrids, the pubescence indicating gene-flow from *L. villosa*. Unfortunately, I missed clues (Gray 1861; Skottsberg 1944) that the type specimen of *L. kauaiensis* was an example of this same hybrid. As a result, not only does the name *L. gaudichaudii* f. *hirsuta* apply to the hybrid, but *L. kauaiensis* as well. The latter name is used here to denote the hybrid, with the addition of the multiplication sign to denote its status as a nothotaxon.

Representative specimens: **KAUA'I. Hanalei:** ridge E of Pihea peak towards Kilohana, *Flynn & DeLappe* 3198 (BISH, F, K, MO, PTBG, US); North Bog along Wainiha pali, *Wood & Perlman* 3672 (F, PTBG). **Waimea:** Nāpali-Kona Forest Reserve, Wai'ale'ale trail, Alaka'i Swamp, Ke'aku River, *Chock* 994 (BISH, NSW); Wai'ale'ale, along trail from "Kauku" [Ke'ākū?], *Cranwell et al.* 3047 *pro parte* (GB); Wai'ale'ale, *Hitchcock* 15437 *pro parte* (US); Wai'ale'ale, *Rock* 5109 (BISH); Wai'ale'ale, Sep 1909, *Rock s.n.* (BISH); Wai'ale'ale, Oct 1911, *Rock s.n.* (BISH); Wai'ale'ale, *Rock* 5823 *pro parte* (BISH); ridge SW of Pihea, on east rim of Kalalau Valley, *St. John et al.* 22945 (DUKE).

3. *Lobelia wahiawa* Lammer, sp. nov. TYPE: HAWAIIAN ISLANDS. KAUA'I: Kōloa District, Wahiawa Swamp near headwaters of Wahiawa Stream, 630 m, open swamp with some shrubby areas, frequent, 24 Apr 1964, *Stauffer & Dehler* 5910 (HOLOTYPE: BISH!; ISOTYPES: A! DUKE! K! US!).

Species *Lobeliae* sect. *Galeatellae* longe cognita sed non perspecta; primo adspectu maxime simile *L. xkauaiensi*, cujus una parens est, sed inflorescentia glabra, calycis lobis apice acutis vel acuminatis, et corollae venatione atro-purpurea differt.

Plant 2–4 m tall. Stem 1–2.5 m tall × 1–10 cm diam.; cicatrices 3–5 mm tall × 4.5–9 mm wide, depressed obtrullate or depressed obovate, the corners rounded. Lamina 17–37 cm long × 1–3.3 cm wide, linear, oblanceolate, or narrowly elliptic, glabrous; margin subrevolute; apex acuminate; base attenuate. Inflorescence 1.5–2.5 m tall, 2–5-branched (rarely unbranched in small plants), each branch 20–85-flowered and cylindrical in outline, its axis blackish purple, glabrous; peduncle sparsely covered with sterile bracts that rapidly decrease in size acropetally; sterile bracts 12–160 mm long × 4–22 mm wide, linear, narrowly elliptic, or lanceolate, the apex acuminate, the base cuneate; floral bracts 16–27 mm long × 3–7.5 mm wide, narrowly elliptic, narrowly oblong, or lanceolate, the apex acute or obtuse and sometimes apiculate, the base cuneate; pedicels 17–35 mm long, of more-or-less equal length throughout. Hypanthium 5–9 mm long × 8–14 mm diam., broadly obconic or rarely almost hemispherical, 1/8–1/12 as long as the corolla, glabrous; calyx lobes 9–15 mm long × 3–6.5 mm wide, triangular, narrowly oblong, or lanceolate, equaling to 3 times longer than the hypanthium, the margin entire, the apex acuminate or acute (rarely obtuse) and sometimes apiculate. Corolla 53–75 mm long, pale purple with dark purple longitudinal stripes, glabrous; tube 18–28 mm long × 6–10 mm diam. at middle, suberect or slightly curved, expanding slightly towards the mouth, 2–4.5 times longer than broad; dorsal lobes 30–48 mm long × 3–5 mm wide, 1.3–2.2 times as long as the tube; ventral lip 25–38 mm long × 11–18 mm wide. Filament tube 57–65 mm long, decurved slightly, 4–5 times longer than anther tube, glabrous; anther tube 4–5 mm diam.; dorsal anthers 12–16 mm long; ventral anthers 9–12 mm long. Capsule 20–28 mm long × 10–14 mm diam.; seeds (Fig. 1C) 1.7–2.5 mm long × 0.6–1.4 mm wide, honey- or chestnut-brown.

Icones.—Rock (1919), pl. 16; Carlquist (1980), p. 245 [left], p. 348 [top left]; Sohmer and Gustafson (1987), fig. 114; Lammer (1990), pl. 57 [lower left]. *Figured specimen.*—Rock (1919), pl. 60 [*Heller* 2888, GH].

Distribution, habitat, and phenology.—Endemic to central Kaua'i, known primarily from the Lowland Wet Mixed Communities (Gagné & Cuddihy 1990) at 570–800 m in the watershed of Wahiawa Stream west of Kāhili (cf., Carlquist 1980, p. 346), but also found in the unique Montane Wet Mixed Community (Gagné & Cuddihy 1990) of the summit bog on Wai'ale'ale at 1100–1590 m. Flowering July to March, fruit ripening December to April. Regarded as "rare" by Wagner et al. (1999), an assessment that includes its hybrid with *L. villosa* (see previous taxon).

Etymology.—The specific epithet is the name of the type locality, used as a noun in apposition; it is Hawaiian for "milkfish place" (Pukui et al. 1974), a reference to widespread *Chanos chanos* (Forsskål) of the Chanidae (Actinopterygii).

Vernacular name.—*Pu'e* (Rock 1919; Pukui & Elbert 1971).

Discussion.—This is the glabrous species that has been known for many years (Heller 1897; Rock 1919; Wimmer 1968; Lammers 1990) as *Lobelia kauaiensis*. However, as noted by Skottsberg (1944), the original description of the basionym of that name (Gray 1861) called for a plant “racemo puberulo; calycis viscosi” and its type specimen indeed conforms to that diagnosis. As a result, this glabrous species has no name and so is named here as a new species.

Representative specimens: **KAUAI. [Kawaihau:** Pōhakupili (*vide* Wawra 1873),] Wawra 2044 (W). **Kōloa:** Wahiawa Bog, *Carlquist* 1980 (RSA); Wahiawa Bog, 26 Nov 1972, *Carlquist s.n.* (RSA); Wahiawa Bog, *Fagerlind & Skottsberg* 6480 (GB, UPS, S); Hanapēpē, in turfosis, *Faurie* 552 (A, BISH, P, W); Wahiawa Bog, *Flynn* 371 (PTBG); Wahiawa Bog, *Flynn* 668 (OS); Wahiawa Bog, *Flynn* 699 (OS); Wahiawa Swamp, *Forbes* 294.K (BISH, US, W); Wahiawa Swamp, Aug 1909, *Forbes s.n.* (BISH); Wahiawa Bog, *Gustafson* 1049 (BISH, RSA); in and near a bog at the head of the Wahiawa, 19 Oct 1895, *Heller* 2888 (F, GH, MO, NY, US); Wahiawa Bog, *Kato* LK-2 (BISH); Wahiawa Bog, *Lammers et al.* 5861 (OS); Wahiawa Bog, 28 Dec 1980, *Lucas s.n.* (RSA); bog above Wahiawa, *MacDaniels* 636 (BH, BISH); Wahiawa Swamp, *Sparre* H.75 (S); Wahiawa Bog area west of Mt. Kāhili, *Stern & Carlquist* 1331 (RSA, US); Wahiawa Bog, *Stern & Herbst* 2942 (PTBG, RSA); Kāhili Swamp, Wahiawa, *St. John et al.* 10849 (A, K, BISH, NSW); Kāhili Bog, Wahiawa, *St. John & Fosberg* 13561 (BISH, POM); west side of Wahiawa drainage below ridge between Hulua and Pu'u'au'uka, *Wood et al.* 1059 (MO, PTBG). **Waimea:** Wai'ale'ale, along trail from “Kauku” [Ke'ākū?], *Cranwell et al.* 3047 *pro parte* (BISH); Wai'ale'ale summit, *Davis & Kores* 113 (A, BISH) & 113a (BISH); Wai'ale'ale, *Hitchcock* 15437 *pro parte* (US); Wai'ale'ale, *Hitchcock* 15499 (US); Wai'ale'ale, *Rock* 5115 (BISH); Wai'ale'ale, *Rock* 5823 *pro parte* (GH); Wai'ale'ale, *Rock* 12845 (BISH, K); Wai'ale'ale, Sep 1909, *Rock s.n.* (NY, US, W); along Alaka'i Swamp Trail, *Stone* 1536 (BISH).

4. *Lobelia koolauensis* (Hosaka & Fosberg) Lammers, comb. et stat. nov. *Lobelia gaudichaudii* var. *koolauensis* Hosaka & Fosberg, Occas. Pap. Bernice Pauahi Bishop Mus. 14:4. 1938. *Galeatella gaudichaudii* var. *koolauensis* (Hosaka & Fosberg) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. *Lobelia gaudichaudii* subsp. *koolauensis* (Hosaka & Fosberg) Lammers, Syst. Bot. 13:506. 1988. TYPE: HAWAIIAN ISLANDS. O'AHU: Ko'olau Range, divide between head of Kawai Nui and Kaipapa'u gulches, rare in open windswept sloping bog, 2600 ft, 31 May 1937, *Hosaka & Fosberg* 1915 (HOLOTYPE: BISH [mounted on 5 sheets]!; ISOTYPES: BISH[2]! US! W!).

Plant 1–2.5 m tall. Stem 1–1.5 m tall × 1.8–3 cm diam.; cicatrices 3–4 mm tall × 6.5–10 mm wide, transversely rhombic, the corners acute. Lamina 11.8–20 cm long × 0.9–2.8 cm wide, linear, oblanceolate, or narrowly elliptic, glabrous or the abaxial midrib pubescent; margin distinctly revolute; apex acute or acuminate; base attenuate. Inflorescence 0.5–1 m tall, 2–7-branched (rarely unbranched in small plants), each branch 12–25-flowered and cylindrical in outline, its axis green, glabrous; peduncle sparsely covered with sterile bracts that rapidly decrease in size acropetally; sterile bracts 20–95 mm long × 4–13 mm wide, narrowly oblong, narrowly elliptic, or lanceolate, the apex acute, the base cuneate; floral bracts 20–48 mm long × 5–10 mm wide, narrowly elliptic or lanceolate, the apex acuminate, the base cuneate; pedicels 22–60 mm long, of more-or-less equal length throughout. Hypanthium 5–10 mm long × 7–11 mm diam., broadly obconic, 1/6–1/8 as long as the corolla, glabrous; calyx lobes 10–22 mm long × 3.5–6 mm wide, narrowly triangular or lanceolate, equaling to 4.4 times longer than the hypanthium, the margin entire, the apex acuminate and sometimes apiculate. Corolla 58–78 mm long, white, glabrous; tube 19–31 mm long × 8–12.5 mm diam. at middle, suberect, expanding slightly towards the mouth, 2–3.5 times longer than broad; dorsal lobes 27–45 mm long × 4.5–6.5 mm wide, 0.9–2.4 times as long as the tube; ventral lip 24–40 mm long × 17–24 mm wide. Filament tube 61–78 mm long, suberect, 4–5 times longer than anther tube, glabrous; anther tube 4–4.5 mm diam.; dorsal anthers 14–16 mm long; ventral anthers 9–10 mm long. Capsule 18–21 mm long × 9–10 mm diam.; seeds (Fig. 1D) 1.5–1.8 mm long × 0.8–1 mm wide, honey-brown.

Icones.—Hosaka and Fosberg (1938), fig. 2; Wimmer (1953), fig. 104a.

Distribution, habitat, and phenology.—Endemic to O'ahu, known only from Montane Wet Shrublands (Gagné & Cuddihy 1990) on the summit of the northwestern Ko'olau Range, between Pu'u Ka'inapua'a and 'Eleao, at 670–860 m. Flowering from late May to October, fruits ripening November to January. Considered “endangered” by Wagner et al. (1999).

Representative specimens: **O'AHU. KO'OLAU MTS.:** Poamoho Trail, Pa'aloa-Wahiawā, *Cowan* 252A (WAB); Poamoho Trail, Iā'ie, *Degener et al.* 11497 (MO, W); top of Poamoho Trail crest at head of Punalu'u Valley, *Fosberg* 13330 (BISH); main divide above Kaipapa'u Gulch, *Fosberg* 14224 (BISH, K); Mānana Trail, NE of Pacific Palisades, 12 Jul 1985, *Obata s.n.* (F, OS); Mānana Trail 1 km from summit, 12 Aug 1996, *Obata et al. s.n.* (BISH, OSH); Mānana Trail 0.8 km from summit, *Obata et al.* 569 (BISH), *Obata et al.* 570 (BISH); Mānana Trail, below summit, *Perlman & Obata* 6484 (BISH, PTBG, US); Mānana Valley, north-facing slope, *Perlman et al.* 17171 (PTBG); Mānana Trail to summit, next ridge north of Mānana, *Wood et al.* 8513 (PTBG).

5. *Lobelia gaudichaudii* A. DC. in DC., Prodr. 7:384. 1839. *Dortmanna gaudichaudii* (A. DC.) Kuntze, Revis. Gen. Pl. 2:972. 1891. *Galeatella gaudichaudii* (A. DC.) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. O'AHU: sommet de la montaignes à gauche de là vallée de Onoruru [i.e., Honolulu], [8–24 Oct 1836, *fide* Kuykendall (1947)] *Gaudichaud s.n.* (HOLOTYPE: P-00520806!; ISOTYPES: GH! G-DC! P-00520807!).

Lobelia gaudichaudii var. *coccinea* Rock, Bull. Torrey Bot. Club 44:238. 1917. TYPE: HAWAIIAN ISLANDS. O'AHU: summit of Mt. Kōnāhuanui, Sep 1912, *leg.* G.W. Shaw, *Rock 12742* (HOLOTYPE: BISH!; ISOTYPES: BISH[3]! GH! US!).

Plant 1–3 m tall. Stem 0.8–2 m tall × 1.3–5 cm diam.; cicatrices 2.5–4.5 mm tall × 7–11 mm wide, transversely rhombic, the corners acute. Lamina 9.5–19.5 cm long × 1.1–2.8 cm wide, oblanceolate, densely long pubescent on the abaxial midrib (rarely glabrous); margin distinctly revolute; apex acute or acuminate; base attenuate. Inflorescence 0.4–0.8 m tall, unbranched, 18–36-flowered and cylindrical in outline, its axis green, glabrous; peduncle sparsely covered with sterile bracts that rapidly decrease in size acropetally; sterile bracts 25–110 mm long × 10–18 mm wide, linear, narrowly elliptic, oblong, or ovate, the apex acuminate or acute, the base cuneate; floral bracts 18–32 mm long × 6–8 mm wide, ovate or lanceolate, the apex acute or acuminate, the base cuneate; pedicels 20–40 mm long, of more-or-less equal length throughout. Hypanthium 6–10 mm long × 7.5–12 mm diam., broadly obconic or campanulate, 1/8–1/9 as long as the corolla, glabrous; calyx lobes 13–18 mm long × 4.5–7 mm wide, ovate or lanceolate, 1.6–2.5 times longer than the hypanthium, the margin entire, the apex acuminate or acute. Corolla 60–65 mm long, red, glabrous; tube 20–30 mm long × 6–11 mm diam. at middle, slightly curved, expanding slightly towards the mouth, 2–4.5 times longer than broad; dorsal lobes 30–40 mm long × 4–5 mm wide, equaling to twice as long as the tube; ventral lip 24–30 mm long × 12–20 mm wide. Filament tube 58–66 mm long, decurved slightly, 4–6 times longer than anther tube, glabrous; anther tube 4–6 mm diam.; dorsal anthers 10–13 mm long; ventral anthers 7.5–10 mm long. Capsule 23–30 mm long × 11–19 mm diam.; seeds (Fig. 1E) 1–1.5 mm long × 0.5–0.7 mm wide, chestnut-brown.

Icones.—Gaudichaud (s.d.), pl. 45; Peale (1848), pg. 152; Rock (1919), pl. 56; Degener (1938b); Murata (1995), figs. 56–57 [seed only]; Smith et al. (1995), fig. 1. *Figured specimen.*—Rock (1919), pl. 57 [holotype of *L. gaudichaudii* var. *coccinea*].

Distribution, habitat, and phenology.—Endemic to O'ahu, known only from Montane Wet Shrublands (Gagné & Cuddihy 1990) on the summit of the southeastern Ko'olau Range, between Pu'u Pauao and Mt. Olympus, at 805–960 m. Flowering from July to October, fruits ripening November to January. Considered “vulnerable” by Wagner et al. (1999).

Representative specimens: **O'AHU. KO'OLAU MTS.:** windward *pali* of Pu'u Kōnāhuanui, *Bishop 1188* (BISH); Kōnāhuanui, 10 Jan 1904, *Bryan s.n.* (BISH); near summit Kōnāhuanui (#2), 30 Jul 1922, *Bryan s.n.* (BISH); main ridge between Kōnāhuanui and Mt. Olympus, *Degener 7965* (NY); Bowman Trail, at divide, *leg.* M. Kerr, *Degener 19218* (NY); near summit of Kīpapa Trail, *leg.* M. Kerr, *Degener 21674* (B, W); *mauka* of Tripler Hospital, *Degener 30174* (MASS); summit of Kōnāhuanui, *Forbes 2180.O* (BISH, MO, NY); *Forbes 2182.O* (BISH); between Punalu'u and Kaipapa'u, 8–13 May 1909, *Forbes & Thompson s.n.* (BISH); peak of Mt. Kōnāhuanui, *Garber 82* (BISH); Mt. Lanihuli peak, *Garber 261* (BISH); Lanihuli, *Garber 262* (BISH); Kīpapa-Waiāhole crest, *Grant 7217* (BISH); summit of Kōnāhuanui, *Hillebrand 72* (K); Kīpapa Gulch, on main divide, *Hosaka 686* (BISH, K); Kōnāhuanui, 100 yd E of East Peak, 13 Oct 1974, *Obata s.n.* (B, BISH); summit of 'Aiea Ridge trail off windward crest, 3 Nov 1974, *Obata s.n.* (BISH); Kīpapa Trail, right ridge of Kīpapa Gulch, *Ozaki 561* (BISH); Punalu'u, *Rock 64* (BISH, GH), *Rock 65* (BISH); Mt. Lanihuli, *leg.* Nelson & Stone, *Rock 10003* (BISH); Kōnāhuanui, *Rock 10003* (BISH); Lanihuli, *leg.* Daingerfield, *Skottsberg 185* (GB, S); about ½ hr Poamoho side of Castle Trail Summit along the Ko'olau Crest Trail, *Stemmermann & Higashino 1207* (BISH); Waipi'o-Waiāhole divide, Kīpapa Gulch, *St. John 12077* (BISH, RSA); S of Pu'u Ka'aumakua, *St. John 20252* (BISH); Pu'u Kōnāhuanui, E. brink, *St. John 20315* (BISH); Kōnāhuanui, *Topping 3223* (NY); [above Honolulu, 25 Sep 1840 – 5 Apr 1841 (*fide* Wilkes 1845),] *U.S. Exploring Expedition s.n.* (GH, US).

6. *Lobelia gloria-montis* Rock, Monogr. Stud. Haw. Lobelioid.: 17. 1919. *Lobelia gaudichaudii* var. *gloria-montis* (Rock) H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:121. 1938. *Galeatella gloria-montis* (Rock) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. WEST MAUI: Pu'u Kukui Mt., 5700 ft, Aug 1910, *Rock & Hammond 8209* (HOLOTYPE: BISH!; ISOTYPES: A[4]! BISH[4]! GH! K! NY! OSH! US! W!). This specimen was referred to in the caption of pl. 58 as “Type;” Hammond is not mentioned as co-collector on many of the isotypes.

Plant 1.5–5 m tall. Stem 0.4–4 m tall × 1.5–10 cm diam.; cicatrices 3–5 mm tall × 6–13 mm wide, transversely rhombic, the corners acute. Lamina 10–24 cm long × 1.3–3.8 cm wide, oblanceolate or narrowly oblong,

glabrous or margin ciliate toward base; margin subrevolute or merely thickened; apex acute or acuminate; base attenuate, cuneate, or obtuse. Inflorescence 1–1.5 m tall, unbranched or 5–7-branched, each branch 18–100-flowered and pyramidal in outline, its axis green, glabrous or pubescent; peduncle sparsely covered with sterile bracts that rapidly decrease in size acropetally; sterile bracts 30–120 mm long \times 10–25 mm wide, oblanceolate, narrowly oblong, oblong, or elliptic, the apex acuminate or acute, the base cuneate; floral bracts 20–90 mm long \times 6–16 mm wide, obovate, elliptic, lanceolate, oblong, or linear, the apex acute or acuminate, the base cuneate; pedicels 15–60 mm long. Hypanthium 8–15 mm long \times 6–17 mm diam., broadly obconic or campanulate, $\frac{1}{5}$ – $\frac{1}{10}$ as long as the corolla, glabrous or pubescent; calyx lobes 7.5–35 mm long \times 3.5–9 mm wide, narrowly triangular or lanceolate, $\frac{3}{4}$ as long to $3\frac{1}{2}$ times longer than the hypanthium, the margin entire and sometimes ciliate, the apex acuminate or acute and sometimes apiculate. Corolla 67–103 mm long, white or rarely red, glabrous (rarely sparsely pubescent at apex of lobes); tube 26–45 mm long \times 7–15 mm diam. at middle, suberect or slightly curved, expanding slightly towards the mouth, 2.2–5 times longer than broad; dorsal lobes 35–70 mm long \times 4–6 mm wide, 0.9–3.1 times as long as the tube; ventral lip 30–52 mm long \times 12–28 mm wide. Filament tube 58–82 mm long, decurved slightly, $4\frac{1}{2}$ – $6\frac{1}{4}$ times longer than anther tube, glabrous; anther tube 4–6.5 mm diam.; dorsal anthers 11–16 mm long; ventral anthers 8–13 mm long. Capsule 27–37 mm long \times 10–18 mm diam.; seeds [Fig. 1F] 2–2.3 mm long \times 1–1.2 mm wide, honey- or chestnut-brown.

Distribution, habitat, and phenology.—Known from Montane Wet Mixed Communities and Montane Wet Forest (Gagné & Cuddihy 1990) on Maui and Moloka'i, where two subspecies occur; see below for details.

6a. *Lobelia gloria-montis* subsp. *gloria-montis*

Lobelia gloria-montis var. *molokaiensis* O. Deg., Fl. Hawaiiensis, Fam. 339. 1938. *Galeatella gloria-montis* var. *molokaiensis* (O. Deg.) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. MOLOKA'I: along Pāpa'alā pali, growing on the fog- and windswept pali, 6 Jun 1928, Degener 7778 (HOLOTYPE: NY!).

Lobelia gaudichaudii f. *bryanii* H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:123. 1938. *Galeatella gloria-montis* var. *bryanii* (H. St. John & Hosaka) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. WEST MAUI: Pu'u Kukui, May 1910, Forbes 68.M (HOLOTYPE: BISH!; ISOTYPES: BISH! NSW! P! US! WI!).

Lobelia gaudichaudii f. *kukuiensis* H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:123. 1938. *Galeatella gloria-montis* var. *kukuiensis* (H. St. John & Hosaka) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. WEST MAUI: Ha'ela'au-Pu'u Kukui trail, brushy opening in rain forest, 4400 ft, 19 Dec 1928, Ewart 89 (HOLOTYPE: BISH!; ISOTYPE: BISH!).

Lobelia gaudichaudii f. *sanguinea* H. St. John & Hosaka, Occas. Pap. Bernice Pauahi Bishop Mus. 14:123. 1938. *Galeatella gloria-montis* f. *sanguinea* (H. St. John & Hosaka) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. TYPE: HAWAIIAN ISLANDS. WEST MAUI: Pu'u Kukui, in swamp, 4500 ft, 16 Aug 1933, Hartt s.n. (HOLOTYPE: BISH!; ISOTYPES: BISH[4]! US!).

Plant 1.5–2.4 m tall. Stem 0.4–1.5 m tall \times 1.5–4 cm diam. Lamina 10–24 cm long \times 1.3–3.8 cm wide, oblanceolate or narrowly oblong. Inflorescence 1–1.5 m tall, unbranched (rarely with 1 or two clearly subordinate basal branches), 18–100-flowered; floral bracts 20–47 mm long \times 6–16 mm wide, obovate, elliptic, or lanceolate; pedicels 15–45 mm long. Hypanthium 8–15 mm long \times 6–17 mm diam., broadly obconic or campanulate, $\frac{1}{5}$ – $\frac{1}{10}$ as long as the corolla, glabrous or rarely pubescent; calyx lobes 7.5–25 mm long \times 3.5–9 mm wide, narrowly triangular or lanceolate, $\frac{3}{4}$ as long to $3\frac{1}{2}$ times longer than the hypanthium. Corolla 67–96 mm long, white or rarely red, glabrous (rarely sparsely pubescent at apex of lobes); tube 26–45 mm long \times 7–13 mm diam. at middle, suberect, 2.2–5 times longer than broad; dorsal lobes 35–70 mm long \times 4–6 mm wide, 0.9–3.1 times as long as the tube; ventral lip 30–48 mm long \times 12–28 mm wide. Filament tube 58–80 mm long, $4\frac{1}{2}$ – $6\frac{1}{4}$ times longer than anther tube; anther tube 4–6.5 mm diam.; dorsal anthers 11–16 mm long; ventral anthers 8–13 mm long. Capsule 27–37 mm long \times 10–15 mm diam.; seeds [Fig. 1F] 2–2.3 mm long \times 1 mm wide, honey-brown.

Icones.—Hitchcock (1919), pl. 25-1; Rock (1919), pl. 15 [right], 17, 18; Degener (1938a); Wimmer (1943), fig. 11d; Wimmer (1953), fig. 104b [seed only]; Degener and Degener (1974), p. 2; Carlquist (1980), pp. 212C [bottom], 245 [right]; Degener and Degener (1983), p. 456; Kepler (1983), p. 80 [upper right]; Sohmer and Gustafson (1987), fig. 121; Lammers (1990), pl. 57 [upper right]. *Figured specimen.*—Rock (1919), pl. 58 [holotype of *L. gloria-montis*].

Distribution, habitat, and phenology.—Known primarily from Montane Wet Mixed Communities (Gagné & Cuddihy 1990) on Pu‘u Kukui, West Maui, at 915–1760 m (cf., Carlquist 1980, p. 352); sterile plants from Montane Wet Shrublands (Gagné & Cuddihy 1990) on eastern Moloka‘i, at 1165–1350 m are placed here as well. Flowering July through December, fruit ripening August through May. Considered “apparently secure” by Wagner et al. (1999).

Representative specimens: **Moloka‘i:** Pāpa‘alā pali, Anderson 513 (BISH); Kalua‘aha Ahu., ridge E of Manawai Gulch, Warshauer & McEl-downey 2390 (BISH). **West Maui:** Mountains, 3 Aug 1961, Bonsey & Suthers s.n. (MSC); Pu‘u Kukui, Bryan 632 (BISH); Pu‘u Kukui, Dec 1928, Bryan s.n. (BISH); below summit, Pu‘u Kukui, Carlquist 553 (RSA); Pu‘u Kukui, Carlquist 555 (RSA); Pu‘u Kukui, Carlquist 2142 (BISH, MICH, RSA); S of Pu‘u Kukui summit, Char & Arakawa PKWM-55-76 (PTBG); Pu‘u Kukui, Cranwell et al. 2667 (BISH, GB, K, S); Pu‘u Kukui, on road to Nākalalua, Cranwell 2668 (BISH, GB, K, S); just below summit of Mt. ‘Eke on northwest side, Degener 7937 (B, BISH, CAS, GH, K, MICH, MO, NY, WIS), Degener 7938a (B, CU, K, MASS, MO, NSW, NY, US, WELC), Degener 7938b (BISH, NY); Pu‘u Kukui summit, Degener et al. 25023 (W); ‘Eke, Forbes 456.M (BISH); Pu‘u Kukui, Gillett 1793 (BISH); trail up to Pu‘u Kukui, Gillett et al. 2444 (BISH); Keahikauō Bog, NE of ‘Eke Crater, Gustafson 2020 (OS, RSA); Pu‘u Kukui, Higashino 76-29 (BISH); summit of Mt. ‘Eke, 1870, Hillebrand s.n. (B); ‘Eke, s.d., Hillebrand s.n. (C, GH, K, NSW, S, US); Pu‘u Kukui, Hitchcock 14735 (US); Pu‘u Kukui, near summit, Hitchcock 14836 (US); Pu‘u Kukui, Hitchcock 14861 (US); from Violet Lake to near the summit, Hobdy 665 (BISH); top of mt., Mann & Brigham 462 (BISH, GH, K); top of mts., Mann & Brigham s.n. (US); ‘Eke trail, base of ‘Eke Crater, Medeiros 341 (BISH); Pu‘u Kukui, McAlpin 635 (DUKE); Mt. Kukui, Munro 418 (BISH); Pu‘u Kukui, Munro 419 (BISH); Pu‘u Kukui, Munro 615 (BISH, K); Pu‘u Kukui, 16 Aug 1933, Neal & Hartt s.n. (BISH); western headwaters of Kahakuloa Str. N of ‘Eke, Oppenheimer & Kunna H119910 (BISH); Violet Lake, Perlman et al. 6884 (MO, PTBG); Pu‘u Kukui, Aug 1910, Rock s.n. (A, NSW, NY); summit of Pu‘u Kukui, Aug 1910, Rock s.n. (NSW, NY); summit of Mt. ‘Eke, Sep 1918, Rock & Hashimoto s.n. (BISH); Pu‘u Kukui, summit bog, Skottsberg 773 (BISH, GB, S); Pu‘u Kukui, St. John 10274 (BISH); Pu‘u Kukui, Tessene 1786 (WIS); Pu‘u Kukui, Wilbur & Webster 834 (DUKE); Pu‘u Kukui summit bogs, Wood 11505 (OSH, PTBG).

6b. *Lobelia gloria-montis* subsp. *longibracteata* (Rock) Lammers, stat. nov. *Lobelia gaudichaudii* var. *longibracteata* Rock, Indig. Trees Haw. Isl.: 78. 1913. *Lobelia gloria-montis* var. *longibracteata* (Rock) Rock, Monogr. Stud. Haw. Lobelioid.: 119. 1919. *Lobelia longibracteata* (Rock) E. Wimm., Pflanzenr. IV.276c: 889. 1968. *Galeatella gloria-montis* var. *longibracteata* (Rock) O. Deg. & I. Deg., Fl. Hawaiiensis, Fam. 339. 1962. *Galeatella longibracteata* (Rock) O. Deg. & I. Deg., Prodr. Galeatella & Neowimmeria: 6. 1974. TYPE (designated by Rock 1913b): HAWAIIAN ISLANDS. WEST MAUI: Mt. Pu‘u Kukui, 5780 ft, Aug 1910, Rock 8818 (LECTOTYPE: BISH!; ISOLECTOTYPES: A! BISH! GH!).

Lobelia gaudichaudii var. *albiflora* H. St. John & A.C. Medeiros, Phytologia 63:366. 1987. TYPE: HAWAIIAN ISLANDS. EAST MAUI: Haleakalā, NE rift on bog margin, above mid-camp bog, “4200 m” [ft], 13 Jun 1982, Medeiros 4 (HOLOTYPE: BISH!).

Plant 2.4–5 m tall. Stem 2–4 m tall × 2–10 cm diam. Lamina 18–23 cm long × 1.8–4.3 cm wide, oblanceolate. Inflorescence 1–1.5 m tall, unbranched or 5–7-branched, each branch 40–80-flowered; floral bracts 60–90 mm long × 6–10 mm wide, oblong or linear; pedicels 38–60 mm long. Hypanthium 10–13 mm long × 11–18 mm diam., broadly campanulate, 1/8 as long as the corolla, pubescent; calyx lobes 25–35 mm long × 5–9 mm wide, narrowly triangular, 2–3½ times longer than the hypanthium. Corolla 78–103 mm long, white, glabrous; tube 28–44 mm long × 12–15 mm diam. at middle, slightly curved, 2.5–3 times longer than broad; dorsal lobes 45–70 mm long × 5–6 mm wide, half again as long as the tube; ventral lip 40–52 mm long × 22–26 mm wide. Filament tube 68–82 mm long, 4.5–5 times longer than anther tube; anther tube 4.5–6 mm diam.; dorsal anthers 15–17 mm long; ventral anthers 11–13 mm long. Capsule 33–36 mm long × 14–18 mm diam.; seeds 2 mm long × 1.2 mm wide, chestnut-brown.

Figured specimen.—Rock (1919), pl. 59 [lectotype].

Distribution, habitat, and phenology.—Known only from Montane Wet Forest (Gagné & Cuddihy 1990) on the rim of ‘Īao Valley, West Maui, at 1740–1760 m; and on the northwestern slopes of Haleakalā, East Maui, at 1280–1700 m. Flowering from June to August.

Representative specimens: **West Maui:** Pu‘u Kukui summit and extending to east bog and Helu Peak along the ridge line, Hobdy 664 (BISH). **East Maui:** NE outer rift on margin of Mid Camp bog, Medeiros 2076 (BISH); S rim of Kīpahulu Valley, Kuiki, Haleakalā, St. John & Mitchell 21237 (BISH).

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